

Note on the Offspring of Thoroughbred Chestnut Mares

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Scawen Blunt* for the Kehailan strain of Arabs. The same assertion is also made for the horses called "*rote*" (? red chestnut) in the Jutland breed by Jensen.† Finally, we have a general statement by Hayes,‡ applicable to all kinds of horses, that in the vast majority of cases a foal from a chestnut dam by a chestnut sire is of a chestnut colour.

The existence of the two kinds of dominants, and the conclusions based thereon have not, so far as I know, been previously recognised.

Note on the Offspring of Thoroughbred Chestnut Mares.

By W. F. R. WELDON, F.R.S.

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The colours of English thoroughbred race-horses, as recorded in Weatherby's General Stud-Book, are grouped under the six main categories—Grey, Roan, Chestnut, Bay, Brown, Black; but each category includes a considerable range of colour, and intermediates occur with quite sensible frequency. At the meeting of the Royal Society, held on December 7 last, the suggestion was made that the relation between the most important colours, Chestnut, Bay, and Brown, might be expressed by a simple Mendelian formula—Bay or Brown being regarded as determined by one Mendelian unit, which was "dominant" to the "recessive" Chestnut. In discussing this suggestion, I made certain statements, which I promised to justify as soon as possible, by offering the data, on which they were based, for publication. The object of the present note is partly to fulfil my promise, and partly to call attention to certain facts which must be considered in the attempt to apply any Mendelian formula whatever to the inheritance of coat colour in race-horses.

I have taken from Weatherby's Stud-Book a fairly complete record of all the foals produced in England by Chestnut mares during the period (rather more than eight years) covered by vols. 18 and 19. All cases of doubtful paternity have been excluded, and I have not tried to obtain external evidence in the few cases where the colour of sire or of foal is omitted. With

* 'The Nineteenth Century and After,' 1906, January, p. 63.

† 'Deut. Pferdezucht,' I, Hft. 11, 1904. (Original not seen; abstract in 'J. B. Landw. Pfl. u. Tierzüchtung,' 1905, II, p. 273.)

‡ 'Points of the Horse' (3rd ed.), 1904, p. 326.

these limitations, I believe the following statements are substantially complete and accurate.

The Chestnut mares recorded produced, in the period dealt with, 5643 foals by 726 sires, the colours of the sires being as follows:—

Colour of sire.	No. of sires.	Colour of sire.	No. of sires.
Ch.	214	Br. or Bl.	10
Ch. or Ro.	2	Bl.	8
Ch. or Bl.	1	Gr.	3
B. or Ch.	1	Ro. or Gr.	1
B.	340	Br. or Gr.	1
B. or Br.	24	Gr. or Bl.	1
Br.	120		
			726

It will be seen that 41 of these sires are intermediate between some two of the accepted colour-categories.

Omitting the Roan or Grey sires, the foals produced are shown in the following table:—

Offspring of Chestnut Mares.

Colour of sire.	Colour and frequency of foals.							Totals.
	Ch.	Int. Ch.	B.	B. or Br.	Br.	Br. or Bl.	Bl.	
Ch.	1568	—	18	2	3	1	2	1594
B.	1118	7	1449	89	132	4	8	2807
B. or Br.	44	1	85	9	21	2	1	163
Br.	233	2	439	44	146	13	14	891
Br. or Bl.	22	—	5	1	5	1	3	37
Bl.	13	—	28	5	11	2	8	67
	2996	10	2024	150	318	23	36	5559

1. *Chestnuts Mated Together.*—It is clear that Chestnut cannot be regarded as a Mendelian recessive, since Bay, Brown, Black, and their intermediates, may be produced by the union of two Chestnut individuals. The number of foals not Chestnut, resulting from such unions, is 26, or about 1 in every 60 of the whole number observed. They were produced by 21 out of the 214 sires recorded, or about 1 sire in every 10 produced at least 1 foal which was not Chestnut. Since the mean number of foals per sire is only $1594/214 = 7.4$ through the period observed, the most probable number of

sires giving foals of colour other than Chestnut, if each sire were capable of giving 1 such foal in 60, would be $7.4/60 \times 214$, or about 26, the standard deviation of the expectation being nearly 4.6; so that the result obtained is not inconsistent with the view that any Chestnut horse is capable of producing, by union with a Chestnut mare, a small proportion of foals of some colour not Chestnut. If each sire had produced but a single foal, we should clearly have to expect that only 1 sire in 60 would produce a foal of abnormal colour. Among the sires recorded, 56 have produced only a single foal each, and of these foals one is Bay or Brown.

On the other hand the Chestnut sires, *Amphion* and *Despair*, have produced 115 foals, all Chestnut, while *Amalfi*, *Brag*, and *Dog Rose* have together produced 36 Chestnuts and seven of other colours during the period examined.

We may conclude: (1) That the mean chance of obtaining a foal which is not Chestnut from two Chestnut parents is about $1/60$; and (2) that this chance is not the same for all sires; it is probably less than $1/60$ for *Amphion*, *Despair*, and their like, and much greater for such sires as *Amalfi*, *Brag*, and *Dog Rose*. This variability in the power of transmitting colours other than their own, possessed by Chestnut sires, is precisely what Galton's theory of dominance would lead us to expect; it is, however, a difficulty in the way of any Mendelian theory involving a reasonably small number of elements.

2. *Chestnuts Mated with Bays and Browns*.—On the view that Bay is a Mendelian "dominant" to Chestnut, Bay sires should be sharply divided into two series: those which are "hybrid," or of constitution "DR," giving 50 per cent. of Chestnut foals and 50 per cent. of Bays by the unions considered, and those which are "pure dominants," giving only Bay offspring. Any Bay horse with one Chestnut parent must be "hybrid" on this view; but it does not follow because both parents are Bay that a Bay colt is a pure dominant. In the table below, those Bay sires which had *either* one Chestnut parent, *or* were known to have produced a Chestnut foal, are classed as "DR"; while a Bay whose parents were both of some colour other than Chestnut was classed as DD unless I could find a record that it had produced a Chestnut foal.

Among the 65 sires classed as DD, no less than 37 have produced only one foal each during the period dealt with. Some of the sires are so young that their whole progeny from Chestnut mares is too small to afford a test of their real nature; others are so old that the labour of testing them by reference to previous volumes of the Stud-Book is great, and involves risk of error. For such reasons as these, the number of sires classed as DD is certainly rather

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above than below the truth. In spite of this, however, the proportion of Chestnut foals produced by the sires called DR is too small for any simple Mendelian theory. The simple Mendelian expectation is half, or 1235 Chestnuts, the standard deviation being $\sqrt{2470/4}$, or about 24·8. The observed deviation is -77, or more than 3·1 times the standard deviation, and a reference to the Tables of the Probability Integral shows that the chance of getting a deviation so great as this is only 0·0009, or a little less than one in a thousand.

Chestnut Mares × Bay Horses.

Sire.	Colour and frequency of foals.									
	Ch.	Ch. Ro.	Ch. Bl.	Ch. B.	B.	B. Br.	Br.	Br. Bl.	Bl.	Totals.
“ DR ”	1118	1	1	4	1141	68	88	4	5	2430
“ DD ”	—	—	—	1	308	21	44	—	3	377
	1118	1	1	5	1449	89	132	4	8	2807

The matings with *Brown* horses, treated in the same way, give similar results.

Chestnut Mares × Brown Horses.

Sire.	Colour and frequency of foals.							
	Ch.	Ch. B.	Ch. Br.	B.	B. Br.	Br.	Br. Bl.	Totals.
"DR"	233	—	—	246	25	72	9	594
"DD"	—	1	1	193	19	74	4	297
	233	1	1	439	44	146	13	891

Here the simple Mendelian expectation is 297 Chestnuts, so that the observed deviation from the required result is - 64, the standard deviation of the expected result being $\sqrt{594/4} = 12·2$, or the observed result is even more improbable than that given by Bay sires.

If we attempt to consider some more complex Mendelian theory of the relation between Chestnut and Bay or Brown, we must base our hypothesis of the number of gametic determinants involved upon some separation of

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sires into groups, those of each group giving a definite proportion of Chestnut foals when mated with Chestnut mares. My observations do not at present decide this point ; but through the period I have dealt with no such separation of sires into groups seems possible. Taking only the Bay or Brown sires which have given at least 20 foals in the period covered by my records, I find—

Sire.	Foals.	
	Ch.	Not.
Oberon	1	42
Blue Green	1	28
Minting	2	31
Veracity	2	29

at one end of the series and at the other such sires as *Rightaway* (21 Ch. + 10 Not), or *Queen's Birthday* (13 Ch. + 3 Not), which offer a transition to such Chestnut sires as *Amalfi*.

The detailed discussion of individual sires, and of the proportion of Chestnuts yielded by each, must be postponed until the work of extracting the records from the Stud-Book has been completed. In the meantime, however, the following points seem clear :—

1. No simple Mendelian view of the relation between Chestnut, Bay, and Brown, regarding Chestnut as a simple recessive, can be maintained.

2. The chance of getting a Chestnut foal from a Chestnut mare is not constant for sires of any colour whatever, and there is no indication that sires of any colour can be sorted into groups such that those in each group will give Chestnut foals in a Mendelian proportion when mated with Chestnut mares.

3. These points, together with the values for parental and grand-parental correlations already given by Professor Pearson* make it probable that the facts of inheritance of coat colour in horses can be expressed in terms of the hypothesis outlined by Mr. Galton in 1872,† and developed by him in his subsequent writings.

I hope to discuss the application of Mr. Galton's hypothesis to these data before long ; but the extraction of pedigrees from the Stud-Book is an operation which takes time, and I have felt bound to offer this imperfect statement in justification of what I said in the discussion to which I have referred, without waiting until my work should be completed.

* 'Phil. Trans.,' A, vol. 195.

† 'Roy. Soc. Proc.,' No. 136, pp. 394—402.